

A MODEL FOR ESTIMATING BUTTERFLY SPECIES RICHNESS OF AREAS ACROSS THE INDIAN SUBCONTINENT: SPECIES PROPORTION OF FAMILY PAPILIONIDAE AS AN INDICATOR¹

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The proportions of species in many of the five butterfly families (Hesperiidae, Papilionidae, Pieridae, Lycaenidae and Nymphalidae) found across the Indian subcontinent show a relatively invariant relationship with the overall butterfly species richness, at both local and regional scales. This relationship suggests that it is possible to use the species total of a single butterfly family best suited to estimate the overall species richness of all other butterflies in an area. Family Papilionidae is a logical choice over others for ease of sampling. Also, there is a strong positive correlation between Papilionidae species richness and the overall species richness of all other butterflies across all other areas, and the proportion of this family is reasonably invariant. The mean proportion (7%) of this family can thus be used to estimate the overall butterfly species richness of an area across the Indian subcontinent for which the Papilionidae species total is known.

Key words: Butterflies, Papilionidae, Indian subcontinent, species richness, spatial distribution

INTRODUCTION

The Indian subcontinent, which includes the area from Baluchistan (Pakistan) eastwards through India up to Myanmar and Sri Lanka, as well as the higher trans-Himalayan zone, is habitat for more than 1,439 species (Evans 1932, Haribal 1992) of butterflies representing 7.2-11.1% of the total world species [13,000 (Owen 1971) - 20,000 (Vane-Wright 1978)]. Amongst these, about 100 species are endemic to the Subcontinent (Smetacek 1996) and at least 26 taxa are today "globally threatened" (IUCN 1990). Identification and prioritisation of areas of conservation concern, i.e. butterfly biodiversity hotspots, are usually based on local endemic and relict taxa, their biogeographical affinities and globally threatened and rare status. However, prioritisation and selection of such areas requires estimation of various ecological indices [e.g. Shannon diversity index, Pielou's evenness index, Similarity index (Ludwig and Reynolds 1988)] which depend on the 'absolute species richness' of the species of the area. Data on the absolute butterfly species richness of most areas across the Subcontinent is non-existent. Traditional methods of deriving species richness by collecting and counting all the species in an area require much time, effort and resources, which were not easily available, and hence such studies have not been carried out in India. There is a need to evolve easy and cost effective methods to estimate the butterfly species richness of areas of concern.

Beccaloni and Gaston (1995) have proposed such a method to predict butterfly species richness of areas

in the lesser known tropical forests of Central and South America, with the help of known species totals of only a single sub-family (Nymphalidae: Ithomiinae) also called the indicator group. This method is based on the fact that the proportions of species in many of the 14 subfamilies and families occurring in these forests show a relatively invariant relationship with the overall species richness of the area, on both local as well as regional scales. Besides, the species richness of this indicator group also has a strong positive correlation with the overall species richness of all the butterflies across the areas and the proportion (4.5%) of this group is reasonably invariant across tropical forests of central and south America. Keeping in mind the findings of Beccaloni and Gaston (1995), the present study was conducted to determine if proportions of butterfly species in families distributed over the Indian subcontinent are also invariant with respect to (i) species richness, (ii) spatial scale, (iii) forest type and (iv) butterfly subregional distribution in the Subcontinent. This study further tries to determine the potential indicator group amongst the 5 major families found in the subregion that can be used to estimate the species richness of other butterflies found in different areas in the Subcontinent.

METHODS

The Indian subregions

The Indian subcontinent (study area) forms a major part of the Oriental region, occupying its extreme

northwestern limits. It has been divided into 9 butterfly subregions (Evans 1932, Wynter-Blyth 1957) as in Fig. 1. (i) Baluchistan or BA (northern limit up to Safed Koh: 26° 00'-34° 00' N and 62° 00'-70° 00' E) and (ii) Chitral or CL (72° 00' E and 36° 00' N) including Chitral, Hunza, Baltistan and Ladakh in both Pakistan and India (iii) western Himalayas or WH (Kashmir: 74° 00' E and 36° 00' N to Kumaon: 80° 00' E and 29° 00' N) in India, (iv) Central Himalayas or CH (Nepal: 80° 00'-88° 00' E to 30° 00'-27° 00' N), (v) Northeast India (includes eastern Himalayas from Sikkim: 88° 00' E and 29° 00' N to Arunachal Pradesh: 96° 00' E and 28° 00' N in India through Bhutan and parts of Bangladesh) and north Myanmar (up to Shan States: 97° 00'-100° 00' E to 28° 00'-20° 00' N) or NEI & NM, (vi) south Myanmar or SM (Karenni Hills: 97° 00' E and 19° 00' N to Victoria Point: 98° 00' E and 10° 00' N), (vii) Peninsular India or PI (Plains and hills of India south of the Himalayas, east of the Indus and west of Brahmaputra), (viii) Sri

Lanka or SL, (ix) Andaman & Nicobar Islands or A&N of India. Butterfly species found in Baluchistan, Chitral and higher reaches (1,000-5,100 m) of the Himalaya (east, central and west) have strong Palaearctic affinities (Central Asian and Chinese subdivisions), whereas butterflies found in the Peninsular Indian, Malaysian and Indo-Chinese subdivisions have strong Oriental affinities. The drier low-lying areas of PI (Deccan and Indogangetic plains) also show affinity with the African region (Evans 1932, Wynter-Blyth 1957).

Methodology

Species totals of all the 5 commonly recognised butterfly families [Hesperiidae, Papilionidae, Pieridae, Lycaenidae and Nymphalidae (Ackery 1984)]. found in the Indian subcontinent were gathered. Literature spanning 117 years (1882-1999) across 69 areas of the Subcontinent was reviewed. However, in this paper, familywise species totals of only 56 areas, collected

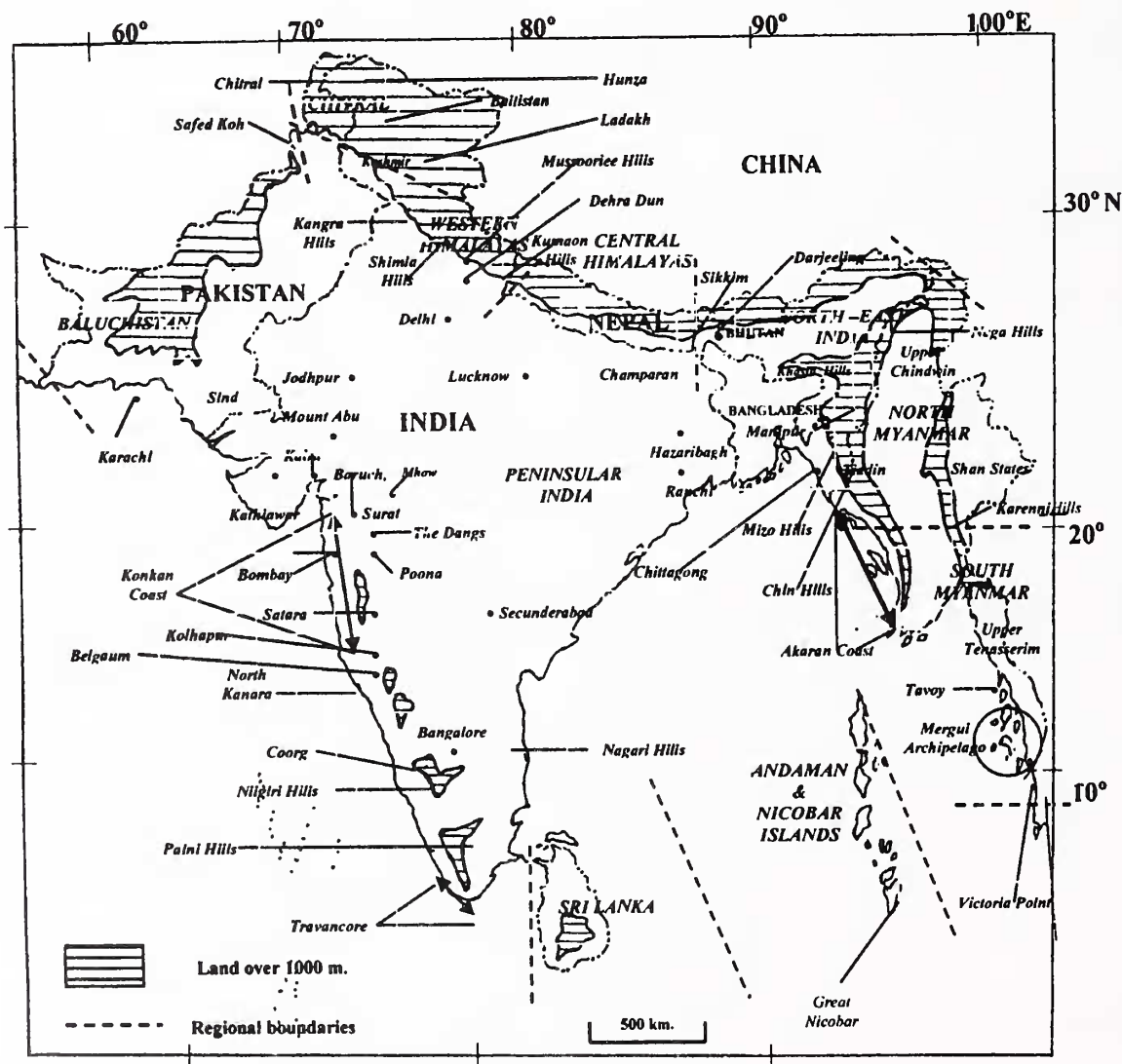


Fig. 1: Nine butterfly subregions of the Indian subcontinent and locations of collection sites

from 45 different sources of literature, have been used, as only these were based on comprehensive surveys for which (i) all the 5 butterfly families were sampled (ii) had a minimum collecting effort of ≥ 2 years (51 areas), (iii) showed no preference to a particular group for collection, (iv) covered all the 9 Indian butterfly subregions and (v) all the 14 major forest types (Champion and Seth 1968) found in the Subcontinent. The scientific names of butterflies used in the old records were updated and the species correctly placed in their respective families, based on the new nomenclature (Ackery 1984). The data was then analysed to derive the proportions of butterfly species in the 5 families from the 56 sites. The areas from which the data were used varied from smallest to the biggest site (sites < districts \leq states \leq sub-regions < the entire Subcontinent), and have been ranked on a spatial scale of 1-7, in an increasing order (Table 1). The details of the areas, their relative size, major vegetation types, collecting (sampling) effort and source of information are given in Table 1. Data on the number of butterfly species per family found in each of these areas is summarised in Table 2. [For one site "Khasia and Jaintia hills" in northeast India, the species totals of 4 families had been published by the authors, leaving out the total for Hesperidae, although collections for all the 5 major families were done. Hence, the regional proportion of Hesperidae (22.2%) for northeast India was taken as an approximate estimate for this site and added to the actual species total (464) of the other 4 families collected (which thus represented 77.8% of the total butterfly species found in this area) to derive the total species richness of this area i.e. 596 species. In this study, the smallest area in the Subcontinent was New Forest, Dehra Dun (4.40 sq. km), which lies in the Tropical Moist Deciduous forest zone of the western Himalaya.

However, the type of data used in this study is prone to error, including unequal sampling effort across areas. Under-recording of species is likely to affect the butterfly totals of the least rich areas more than those of the richest areas. At the site level, however, under-recording is likely to be greatest at the richest area.

RESULTS AND DISCUSSION

Patterns in Species Richness

The proportions of at least 3 out of the 5 families (Papilionidae, Lycaenidae and Nymphalidae) are more or less independent of the total species richness, or size of the area, or forest type, or butterfly subregion, in the Indian subcontinent (Table 2; Figs. 2, 3). The comparatively invariant relationship exhibited by these

families is simpler than the relationships shown by families Hesperidae and Pieridae. The proportion of Hesperidae increases with the total species richness, whereas that of Pieridae decreases (Fig. 2). This variation for these two families is more pronounced across the continuous mountainous subregions [Baluchistan-Chitral-Himalayas (western-central-eastern)-Hills of Myanmar (north-south)] (Fig 1). The proportion of Hesperidae, in general, increases from Baluchistan towards south Myanmar [BA(11.8) - CL (8.4) - WH (15.1) - CH (20.1) - NEI & NM (21.9) - SM (24.0)], whereas that of Pieridae decreases across the same region [BA (21.8) CL (18.1) - WH (10.1) - CH (9.9) - NEI & NM (5.9) - SM (5.1); Table 2].

As proportions of the first 3 families are invariant and show a simple relation to the total species richness, it is possible to use the known species totals of the most suitable of these three groups in an area to estimate the total butterfly species richness of that area. Also, none of these 3 groups show 'saturation' (Beccaloni and Gaston 1995), as their proportions do not decrease with the increase in total species richness. Therefore, all three are potential indicator groups.

Selecting an indicator group

For a group to be an indicator, there should be low variance in the relationship between the species richness of this group and that of the group we wish to predict (Beccaloni and Gaston 1995). Amongst the 3 families identified as potential indicators, Papilionidae ($\bar{x} = 7.0301$; SD = 1.1879; n = 51; CV = 16.90) and Lycaenidae ($\bar{x} = 29.0151$; SD = 3.6779; n = 51; CV = 12.68) have low variance values ($s^2 < \bar{x}$) for proportion (arcsin transformed) of species in families across the Subcontinent, as compared to Nymphalidae ($\bar{x} = 33.4740$; SD = 05.9583; n = 51; CV = 17.80) which exhibits a comparatively large variance ($s^2 \geq \bar{x}$) across the same region. Thus, families Lycaenidae and Papilionidae are more suitable potential indicator groups than Nymphalidae for predicting species richness across the Subcontinent.

Why choose Papilionidae over Lycaenidae as indicators?

Papilionidae (commonly called Swallowtails) are taxonomically and ecologically well known in the Indian subcontinent, and the distribution of practically all the species is known. In contrast, many of the species in Family Lycaenidae are very difficult to identify and very little is known about their life history and ecology because of their obscure habits. Swallowtails (as the name suggests, most of them have tails on their hind wings) are (i) large in size (wing span: 5 - 19 cm for

Table 1: Details of the areas taken in this study and sources from which the butterfly totals in Table II were obtained

Sl. No.	Areas	Area covered (spatial scale: 1-7)*	Major Vegetation Types ** (01-14)	Collecting effort	Sources
1.	Indian subcontinent (61° - 100° E, 5° - 37° N)	7	01-14	Over 100 years (Cumulative)	Evans (1932); Haribal (1992)
2.	Baluchistan	6	10	Over 100 years (Cumulative)	Evans (1932); Wynter-Blyth (1957)
3.	Chitral (Chitral, Hunza, Baltistan and Ladakh)	6	10, 13, 14	Over 100 years (Cumulative)	Evans (1932); Wynter-Blyth (1957)
4.	Chitral	5	10, 13	Feb. 1900-Nov. 1901	Leslie and Evans (1904)
5.	Western Himalaya (Kashmir-Kumaon)	6	03, 09, 12, 13, 14	Over 100 years (Cumulative)	Evans (1932); Wynter-Blyth (1957)
6.	Kangra Hills district	4	05, 09, 10, 12	Several years	Moore (1882)
7.	Shimla Hills (Kinnaur, Kullu, Shimla, Solan, Kalka districts and Chandigarh)	5	06, 09, 12, 13, 14	>19 years (Cumulative)	Wynter-Blyth (1940; 1945)
8.	Dehra Dun Valley (New Forest Campus)	1	03	6 years (1988-92; 1997-98)	Singh (1999)
9.	Mussoorie Hills and neighbouring areas (Uttarkashi, Tehri Garhwal, Dehradun districts)	5	03, 09, 12, 13, 14	11 years (1887-1898)	Mackinnon and deNiceville (1899)
10.	Mussoorie Town	2	12	Several years (consecutive)	Ollenbach (1930)
11.	Kumaon Hills (Almora, Nainital and Pauri Garhwal districts)	5	03, 09, 12, 13, 14	>2 years (1908-1909 and before)	Hannington (1910)
12.	Central Himalaya (Nepal)	6	03, 09, 12, 13, 14	Over 100 years (Cumulative)	Haribal (1992)
13.	North-East India + North Myanmar	6	01, 02, 03, 08, 09, 11, 14	Over 100 years (Cumulative)	Evans (1932)
14.	Northeast India (Sikkim, Bhutan, Assam-Chittagong)	6	01, 02, 03, 08, 09, 11, 14	Over 100 years (Cumulative)	Wynter-Blyth (1957)
15.	Sikkim	4	09, 11, 12, 13, 14	>40 years (cumulative, mainly from 1880-1920 thereafter)	Haribal (1992)
16.	Darjeeling district	4	02, 03, 08, 11, 12, 14	Several years (consecutive)	Maude (1949)
17.	Naga Hills (Nagaland)	4	01, 08, 09, 11	(1889-1890 and thereafter)	Tyler (1911-12)
18.	Manipur and Naga Hills	5	01, 08, 09, 11	3 years (consecutive)	Tyler (1914)
19.	Khasia Hills (Meghalaya)	5	01, 03, 08, 09, 11	3 years	Swinhoe (1893)
20.	Khasia and Jaintia Hills	5	01, 03, 08, 09, 11	>2 years (before and 1948-1949)	Parsons and Cantlie (1951)
21.	Chin- Lushai (Mizoram) Hills	4	02, 03, 08, 09	Oct. 1889 - May 1890	Watson (1891)
22.	N. Chin and Upper Chindwin district	4	02, 03, 08, 09, 11	(Jan-June, 1893)	Watson (1897)
23.	Arakan Coast	4	01, 08	Nov. 1944 - June 1945	Gladman (1949)
24.	Shan States	5	01, 02, 03	1887-1888	Neville Manders (1890)
25.	South Myanmar	5	01, 04, 08	Over 100 years (Cumulative)	Evans (1932)
26.	Upper Tenasserim (Rangoon, Paungde and Bilin)	5	02, 03, 08	Sept. 1885 - Dec. 1886	Watson (1886)

Table 1: Details of the areas taken in this study and sources from which the butterfly totals in Table II were obtained (contd.)

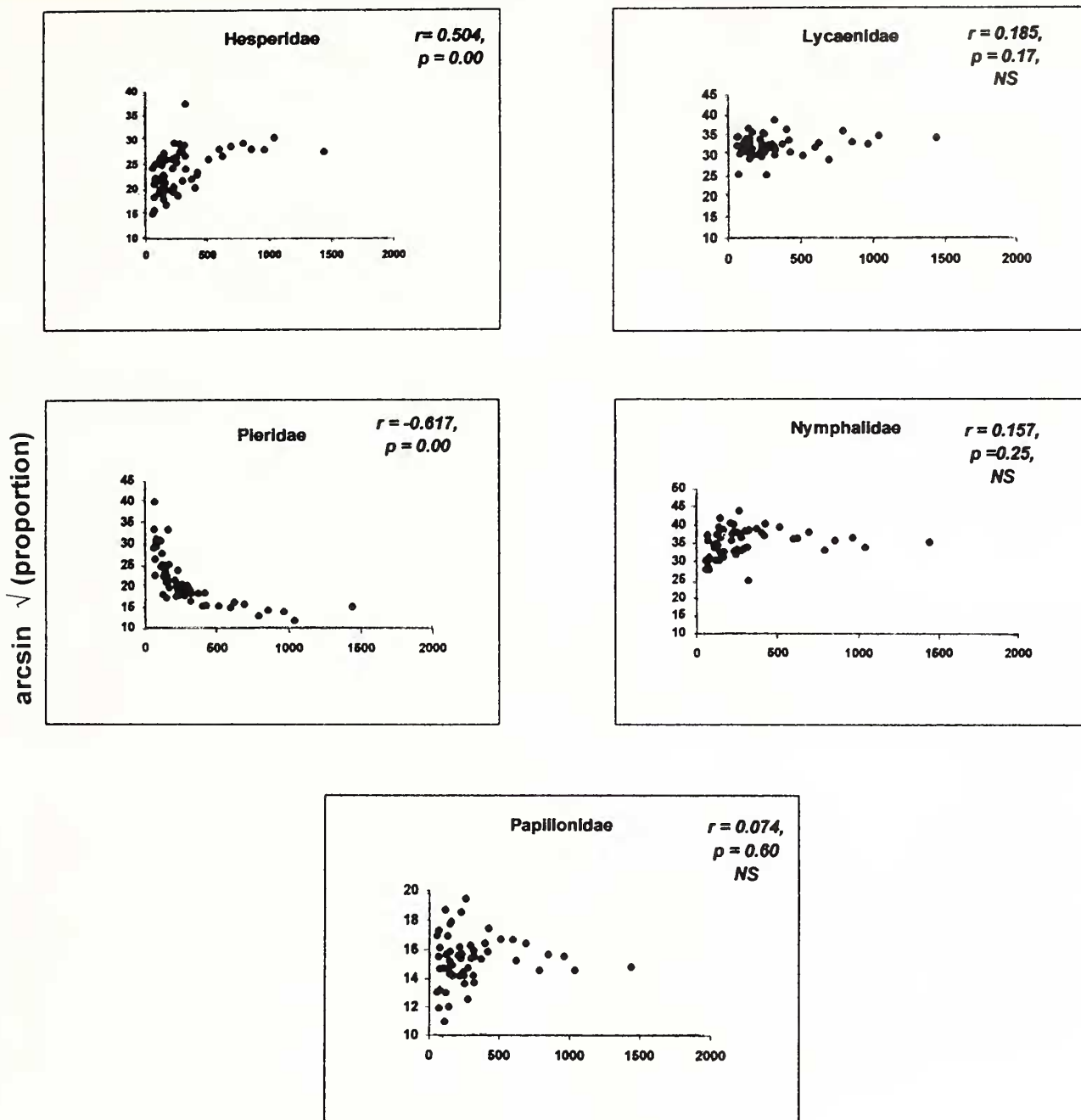
Sl. No.	Areas	Area covered (spatial scale: 1-7)*	Major Vegetation Types ** (01-14)	Collecting effort	Sources
27.	Tavoy District	5	01, 02, 04	10 years (1910-1920)	Ollenbach (1920)
28.	Mergui and its Archipelago	4	01, 02, 04	Expedition?	Moore (1886)
29.	Myanmar	6	01, 02, 03, 04, 05, 06, 08, 09	Over 100 years (Cumulative)	Haribal (1992)
30.	Peninsular India (West, Central and South of Subcontinent)	7	01, 02, 03, 04, 05, 06, 07, 08, 11	Over 100 years (Cumulative)	Evans (1932); Wynter-Blyth (1957)
31.	Central Provinces (mainly Madhya Pradesh and drier parts of Orissa and Maharashtra)	6	03, 05	Several years (consecutive)	Betham (1890-92)
32.	Calcutta	2	02	Several years (consecutive)	Sanders (1944) and Sevastopulo (1944)
33.	South Bihar (Patna, Ranchi, Hazaribagh and Manbhum districts)	4	03, 05	Several years (consecutive)	Morrison-Godfrey (1950)
34.	North Bihar (Champaran district)	4	03	Several years (Sept. - May; before 1950)	Harman (1952)
35.	Lucknow	4	05	4 years (consecutive)	DeRhe-Philippe (1902)
36.	Delhi	4	06	4 years (1961-65)	Donahue (1966 -1967)
37.	Mhow	2	05	1 year (1881-1882)	Swinhoe (1886)
38.	Jodhpur and Mount Abu	3	05, 06, 08	3 years (1920, 1924-25)	Macpherson (1927)
39.	Karachi	3	06	2 years (1878-1880)	Swinhoe (1884)
40.	Sind Province	6	06	15 years (1932-1947)	Menesse (1952)
41.	Central Gujarat (Kathiawar)	5	05, 06	2 years (Dec. 1927 - March 1929)	Mosse (1929)
42.	North Gujarat (Kedar/Kaira district)	4	06	3 years (1941-44)	Aldrich (1949)
43.	South Gujarat (Bharuch, Surat and Dangs districts)	5	03, 06	17 years (1946-1963)	Shull (1963)
44.	Bombay-Deccan (mainly Poona and forested parts of Satara, Kolhapur, Belgaum and Ahmednagar districts)	4	01, 02, 03, 05, 06, 08	>2 years (1982-3; 1877)	Swinhoe (1885)
45.	Konkan Coast	5	02, 03, 08	Several years (1885-1902, cumulative)	Aitken and Comber (1903)
46.	North Kanara district (Uttar Kannada)	5	01, 02, 03	>2 years (1891-1892)	Davidson et al. (1896-1897)
47.	Coorg (Kodagu) district	4	01, 02	>11 years (before 1927, 1927-1929)	Yates (1931-32)
48.	Bangalore district	5	05	3 years (1925-1927)	Yates (1933)
49.	Travancore (Kerala and South Tamil Nadu)	5	01, 02, 03	13 years (1878-1891)	Ferguson (1891)
50.	Palni Hills	3	03, 08, 11	10 years (1950-1960)	Ugarte and Rodericks (1960)

Table 1: Details of the areas taken in this study and sources from which the butterfly totals in Table II were obtained (contd.)

Sl. No.	Areas	Area covered (spatial scale: 1-7)*	Major Vegetation Types ** (01-14)	Collecting effort	Sources
51.	Nilgiri Hills	4	03, 08, 11	Several years (cumulative, based on Hampson, 1888 list)	Wynter-Blyth (1944; 1947)
52.	Nagalapuram Hills (Eastern Ghats: Nagari-Kalahasti)	4	07	1.5 years (August 1950 - Feb. 1952)	Best (1958)
53.	Secunderabad	3	06	1 year (1933-34)	Logan Home (1935)
54.	Sri Lanka	5	01, 02, 08, 11	Over 100 years (Cumulative)	Haribal (1992)
55.	Andaman and Nicobar Islands	4	01, 02, 03, 04	Over 100 years (Cumulative)	Evans (1932); Wynter-Blyth (1957)
56.	Great Nicobar Island	4	01, 02, 03, 04	Several years (1979-1993 cumulative)	Chandra and Khatri (1995)

*Spatial Scale (sq. km): 1 = <10; 2 = >10-100; 3 = >100-1,000; 4 = >1,000-10,000; 5 = >10,000-1,00,000; 6 = >1,00,000-10,00,000; 7 = >10,00,000

** Vegetation (Forest) Types (Champion and Seth, 1968): 01-Tropical Wet Evergreen; 02 - Tropical Semi Evergreen; 03 - Tropical Moist Deciduous; 04 - Littoral and Swamp;
05 - Tropical Dry Deciduous; 06 - Tropical Thorn Forest; 07 - Tropical Dry Evergreen; 08 - Sub-tropical Broad-leaved Hill; 09- Sub-tropical Pine; 10 - Sub-tropical Dry
Evergreen; 11- Montane Wet Temperate; 12 - Himalayan Moist Temperate; 13 - Himalayan Dry Temperate; 14 - Sub-Alpine or Alpine



Total number of species

Fig. 2: Relationship between the proportions of species in a given butterfly family (arcsine transformed) and overall butterfly species richness of collection sites (n=56) across the Indian subcontinent

Indian species) (ii) very active and strong fliers during daylight, when they can be observed flying, or feeding on flower nectar, or mud puddling, but seldom concealing themselves in foliage or settling down to rest, and are also (iii) eyecatching and colourful, with contrasting black as their base colour. In contrast, most of the Lycaenidae are (i) very small or medium sized (wing span: 1.5 - 6 cm. for Indian species) (ii) cannot be easily identified in flight or even at rest, as allied species of the same genus have similar patterns on the underside of

the wings and (iii) are not active fliers like Papilionidae, as they are unable to fly for long stretches and soon settle down to rest (Haribal 1992, Wynter-Blyth 1957). Also, Papilionidae with 94 species (7.01%) is also a smaller group to monitor than Lycaenidae with 459 species (29.22%) (Table 2). All these unique characters of Papilionidae make it an easier group to observe, identify and sample than Lycaenidae.

Besides, the average life span of adult Indian Papilionids ranges from 20-30 days to a maximum of

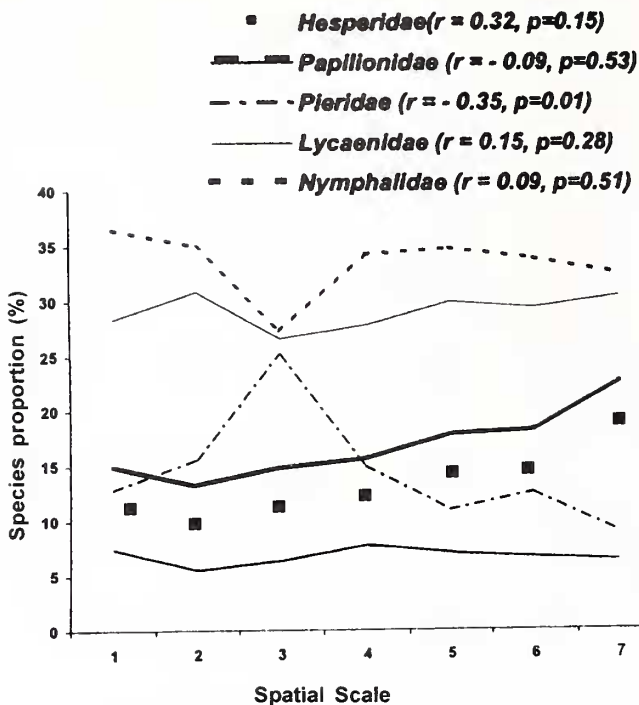


Fig. 3: Relationship between the proportion (%) of species in different families of butterflies and the spatial distribution of collection sites (n=56). Geographical scale (sq. km) 1. <10, 2. >10 to 100, 3. >100 to 1000, 4. >1000 to 10,000, 5. >10,000 to 1,00,000, 6. >1,00,000 to 10,00,000, 7. >10,00,000

4 months (Haribal 1992). Their flight period in the plains ranges from January to December with many overlapping generations, whereas in the hills they fly during summer, between April to September, and have 1-3 generations (Wynter-Blyth 1957), thus Papilionidae can be sampled for a longer period in the year. Papilionidae are found in all types of habitats (gardens, forests, open areas, etc.) from the low lying Indian plains to as high as 5,100 m above msl in the Himalaya (Common Blue Apollo *Parnassius hardwickei* Gray)

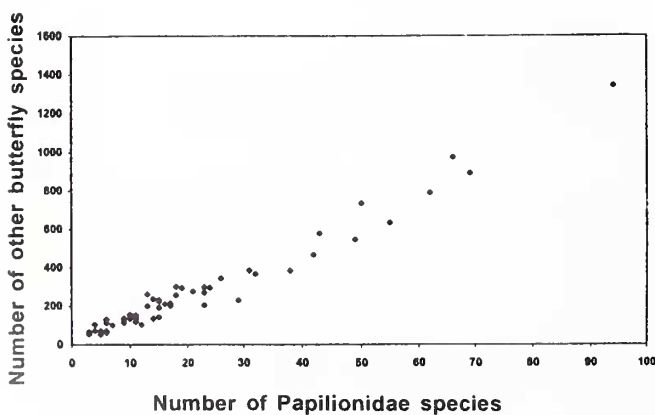


Fig. 4: Plot of butterfly species richness (excluding Papilionidae) versus Papilionidae species richness for sites (n=56) across the Indian subcontinent

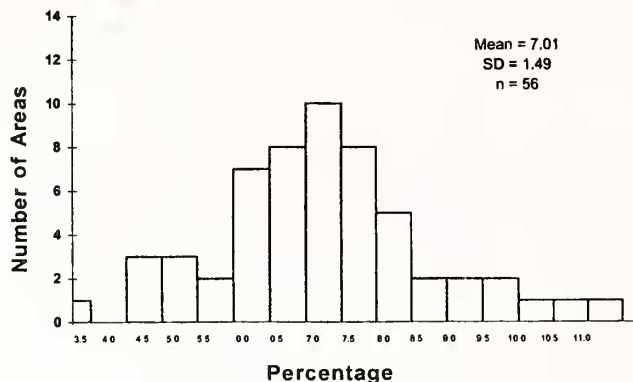


Fig. 5: Distribution of the Papilionidae proportions of different collection sites (n=56) across the Indian subcontinent

(Wynter-Blyth 1957). A large proportion (14.5%) of the worldwide total of 650 Papilionid species is known to occur in the Indian subcontinent (Haribal 1992). Papilionid species richness in the Indian subcontinent peaks in NEI & NM where a large concentration is found [Sikkim (55 species in 7,299 sq. km: Haribal 1992); North-east India (62 species in 3,68,000 sq. km) and Myanmar (66 species in 6,76,577 sq. km): Wynter-Blyth 1957].

Are Papilionidae good indicators for predicting species richness?

A strong positive relationship exists between Papilionidae species richness and the overall species richness (of all the other butterfly families) across 56 different areas over the entire Indian subcontinent, and varying on different spatial scales [(1-7; Table 1) and ($r = 0.980, n = 56, p < 0.01$; Fig. 4). The histogram

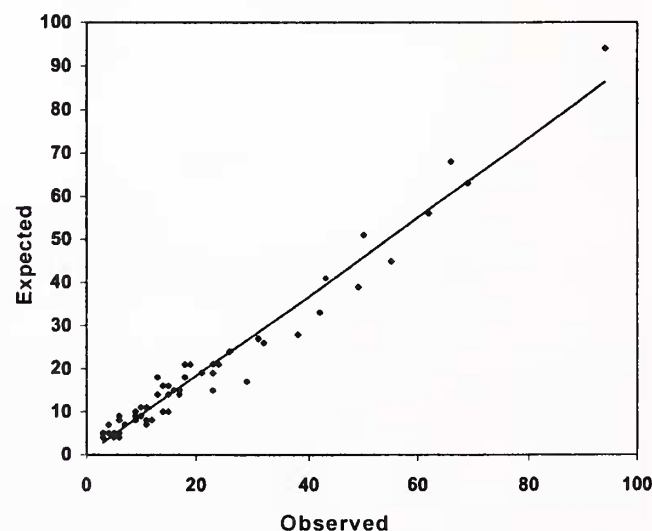


Fig. 6: Relationship between the number of Papilionidae observed and expected to occur in different sites across the Subcontinent (expected values based on the assumption that Papilionidae constitute an invariant proportion of the total butterfly species found across the entire Subcontinent)

Table 2: Total butterfly species richness of areas in the Indian subcontinent and the proportion of species recorded in the families

Sl.no.	Area	Total Species	Percentage of total				
			Hesperiidae	Papilionidae	Pieridae	Lycaenidae	Nymphalidae
1.	Indian subcontinent	1439	21.3 (307)	06.5 (94)	06.9 (99)	31.8 (459)	33.3 (480)
2.	Baluchistan	119	11.8 (14)	05.0 (6)	21.8 (26)	28.6 (34)	32.8 (39)
3.	Chitral	166	08.4 (14)	06.6 (11)	18.1 (30)	27.7 (46)	39.2 (65)
4.	Chitral	139	10.8	04.3	15.8	28.8	40.3
5.	Western Himalaya	417	15.1 (63)	07.4 (31)	10.1 (42)	30.9 (129)	36.5 (152)
6.	Kangra Hills	228	11.0	10.1	16.2	24.6	38.2
7.	Shimla Hills	299	13.7	07.0	11.4	29.4	38.5
8.	Dehra Dun Valley (New Forest)	148	14.9	07.4	12.8	28.4	36.5
9.	Mussoorie Hills and adjoining areas	323	16.7	07.1	09.9	27.3	39.0
10.	Mussoorie Town	146	09.6	06.8	08.9	30.1	44.5
11.	Kumaon Hills	371	14.0	07.0	10.0	29.4	39.6
12.	Central Himalayas (Nepal)	623	20.1 (125)	06.9 (43)	07.9 (49)	29.7 (186)	35.3 (220)
13.	North-East India + North Myanmar	962	21.9 (211)	07.2 (69)	05.9 (57)	29.5 (283)	35.5 (342)
14.	Northeast India	853	22.2	07.3	06.1	30.2	34.2
15.	Sikkim	690	23.0	08.0	07.4	23.5	38.1
16.	Darjeeling district	262	10.3	11.1	12.2	18.3	48.1
17.	Naga Hills	423	15.9	09.0	07.1	26.0	41.8
18.	Manipur and Naga Hills	321	37.1	05.6	00.3	39.2	17.8
19.	Khasia Hills	510	19.2	08.2	07.0	25.0	40.5
20.	Khasia and Jaintia Hills	596	22.2	08.2	06.7	27.8	34.7
21.	Chin- Lushai (Mizoram) Hills	276	21.4	04.7	09.4	27.9	35.5
22.	N. Chin and Upper Chindwin district	320	20.3	07.5	08.1	25.3	38.8
23.	Arakan Coast	159	13.2	09.4	13.2	26.4	37.7
24.	Shan States	228	12.3	07.0	11.0	28.1	41.7
25.	South Myanmar	788	24.0 (189)	06.3 (50)	05.1 (40)	34.5 (272)	30.1 (237)
26.	Upper Tenassrum	252	19.8	05.6	10.7	26.2	37.7
27.	Tavoy district	401	12.0	08.0	07.0	35.1	37.9
28.	Mergui and its Archipelago	208	11.5	07.2	13.5	25.5	42.3
29.	Myanmar	1039	25.6	06.3	04.2	32.5	31.3
30.	Peninsular India	315	23.5 (74)	06.0 (19)	10.8 (34)	28.6 (90)	31.1 (98)
31.	Central Provinces	147	21.1	06.1	13.6	23.8	35.4
32.	Calcutta	167	19.2	06.0	11.4	34.1	29.3
33.	South Bihar	124	14.5	07.3	09.7	37.1	31.5
34.	North Bihar	151	12.9	06.8	15.0	25.2	40.1
35.	Lucknow	109	13.8	06.4	17.4	30.3	32.1
36.	Delhi	77	14.3	05.2	26.0	28.6	26.0
37.	Mhow	110	10.9	03.6	26.4	28.2	30.9
38.	Jodhpur and Mount Abu	78	17.9	07.7	26.9	25.6	21.8
39.	Karachi	70	12.9	04.3	41.4	18.6	22.9
40.	Sind Province	59	16.9	05.1	23.7	32.2	22.1
41.	Central Gujarat (Kathiawar)	78	14.1	06.4	24.4	28.2	26.9
42.	North Gujarat (Kaira)	59	06.8	08.5	30.5	28.8	25.4
43.	South Gujarat	145	15.2	06.9	17.2	31.7	29.0
44.	Bombay-Deccan (Pune)	164	11.6	06.1	30.5	25.0	26.8
45.	Konkan Coast	130	17.7	08.5	14.6	26.9	32.3
46.	N. Kanara district	233	24.0	07.3	09.4	29.6	29.6
47.	Coorg	278	21.6	06.5	11.2	28.8	29.9
48.	Bangalore district	140	14.0	06.4	17.9	35.7	25.7
49.	Travancore	220	16.8	06.8	11.8	26.4	37.3
50.	Palni Hills	249	18.5	06.0	12.0	33.3	30.1
51.	Nilgiri Hills	294	21.8	07.8	11.9	27.9	30.6
52.	Nagalapuram Hills (Eastern Ghats)	117	19.7	10.3	17.9	26.5	25.6
53.	Secunderabad	70	10.0	07.1	20.0	28.6	34.3
54.	Sri Lanka	242	19.8 (48)	06.2 (15)	12.0 (29)	33.9 (82)	28.1 (68)
55.	Andaman and Nicobar Islands	217	19.4 (42)	06.0 (13)	09.2 (20)	31.3 (68)	34.1 (74)
56.	Great Nicobar Island	68	07.3	08.8	14.7	32.4	36.8

Values in parenthesis are species totals for nine butterfly sub-regions and the whole of the Indian subcontinent so far known

(Fig. 5) demonstrates that the variance of Papilionidae proportions across these areas is reasonably low, with Papilionidae constituting 6-8% of the butterfly species in 28 out of 56 areas (and 6.5-7.5% in 18 out of 56 areas) in the Subcontinent.

Five areas [Mhow, Chitral, Chin-Lushai (Mizo) Hills, Darjeeling Hills and Nagalapuram (Nagari) Hills; Table 2] could have been excluded from this analysis, thereby increasing the level of correlation. The first three have the lowest proportions of Papilionidae (Mhow 3.6%, Chitral 4.3% and Chin Lushai 4.7%) of all areas. Data of Mhow and Chin-Lushai suffer from sampling error as less than one year of collecting effort was undertaken. However, data from Chitral also includes a large number of Palaearctic species besides the Oriental species (as this region has strong affinities with the Palaearctic region), which are likely to decrease the proportion of Oriental species. The last two areas, on the other hand, have the highest proportions of Papilionidae of all areas [Nagalapuram Hills (10.3%) and Darjeeling (11.1%)]. Data from Nagalapuram Hills (with only 1.5 years of sampling) is also under-sampled, particularly for Nymphalidae (Table 2). On the other hand, the exact sampling period for Darjeeling district is not mentioned in the original text (Maude 1949) but the data reflects low sampling of species from this area, particularly those of the families Hesperidae and Lycaenidae (Table 1).

A combined data set for sites, districts, states and regions was tested against random draw model in which the proportion of Papilionidae in each area was assumed to equal that for the whole of the Subcontinent (6.5%). Correlation between the number of Papilionid species

observed and expected to occur in each area is high ($r = 0.982$; $n = 55$, $p = 0.001$) and the relationships are fitted by a slope of 1 (Fig. 6).

CONCLUSION

A reasonably invariant relationship exists between proportions of Papilionid species and the overall butterfly species richness across the Indian subcontinent, independent of (i) the different butterfly sub-regions (ii) forest types found in the region (iii) different spatial scales and (iv) species richness of areas. This suggests that it should be possible to use the average proportion (7%) of this family to estimate the butterfly species richness of areas across the Indian subcontinent, for which the Papilionidae species total is known. Using the figure for the overall butterfly richness of an area, approximate estimates for the species totals of the individual butterfly groups in the area can be generated on the basis of known relationships between total butterfly species richness and the species richness of the groups across all areas (provided that these are strong). In the Indian subcontinent, the species richness of at least three families, Papilionidae, Lycaenidae and Nymphalidae, show little variation, and their regional proportions can be used to estimate the species totals. However, for families such as Hesperidae and Pieridae, that show a larger variance across the 9 butterfly sub-regions in the Indian subcontinent, sub-regional proportions are already known (Table 2) and would give more precise estimates of this relationship for predicting the species richness of the respective families.

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